

The Development of the Starfish *Crossaster papposus*, Müller and Troschel.

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With Plate 10 and 12 Text-figures.

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THE development of *Crossaster papposus*, though less important than that of starfish having feeding larvæ, nevertheless presents features of great interest, especially in regard to the origin of the primary larval cœlomic cavities, the madreporic vesicle, the extra rays, the skeleton, and the general modifications due to yoliness of the egg. *Crossaster papposus* much resembles *Solaster endeca* in

development, and accordingly I may be allowed to refer to a former paper on the latter (7) for details and illustrations which do not call for repetition (see, e. g., p. 3 and p. 34).

The Crossasters and Solasters are members of the Solasteridæ, a family of Cryptozonia in the classification of Sladen (23), and of Spinulosæ in that of Perrier (22). In this family the abactinal skeleton is more or less regularly reticulate, many of the plates bearing paxilliform groups of spines; single interbranchial septa are present; there are no pedicellariæ and no supradermal membranes: actinal intermediate plates occur, more or less developed; the adambulacral armature is pectinate, a transverse series being present in all, and also a longitudinal in some.

The two common British species *Crossaster papposus* and *Solaster endeca* show the following differences: In the former the abactinal reticulum is somewhat widely meshed, and the groups of paxillæ are spread well apart, each having relatively few but large spines; the papules are numerous; the number of rays is ± 12 (18); the colour of the abactinal surface is a brighter or darker red, often shading into orange or yellow, especially on the rays. In *Solaster endeca*, on the other hand, the abactinal reticulum is somewhat narrow and irregular, the nodal plates being often stellate in shape; the paxillæ are small and closely crowded; the papules are few, the number of rays is ± 9 (18); the colour of the abactinal surface is a rich purple.

Among the resemblances between *Crossaster papposus* and *Solaster endeca* which are of systematic or structural importance and have not been indicated above we may note the following: The adambulacral armature is in two series, one at right angles to the other; no actinal intermediate plates occur along the rays, and there is one series of well-developed marginal paxillæ (23, p. 442). The madreporite is single and may carry spines; the tube-feet are biserially arranged; a Polian vesicle and two Tiedemann's bodies are present in all the interradii except in the madreporic interradius where one of the latter is wanting: the anus is in interradius V/VI,¹ no matter what may be the number of rays; the rectal cæca are well developed and of similar form; the cilia everywhere exhibit similar activities.

¹ The madreporite is reckoned as lying in interradius I/II, ray I being on its sinistral side. Throughout this paper "dextral" and "sinistral" indicate respectively the sides towards which, or away from which, the hands of a watch would appear to move on a starfish disc as viewed aborally.

Crossaster and Solaster have evidently long been separated from one another since both are widely distributed. Solaster, however, has the greater range, both geographically and bathymetrically, and as it has fewer rays and includes a somewhat greater number of species, we may conclude that it is probably the more primitive of the two genera. The earliest known Solaster is a thirty-rayed form (*S. moretonis*, Forbes) occurring in the oolite (5).

The five-rayed *Cribrella*, though it is placed in another Cryptozoonate family, the Echinasteridæ (23), agrees with Solaster in its chief characters excepting the number of rays. In development *Cribrella* (Masterman, 19, 1902) and Solaster (Gemmill, 7, 1912) show close parallelism excepting as regards the madreporic vesicle (p. 168).

EARLY DEVELOPMENT UP TO GASTRULATION.

The gonads are bunches of short, unbranched, lobulated or very simply branched tubes, reddish or orange in colour, paler in the males, confined to the disc, and not extending out into the arms.

(For details regarding genital ducts, growth of ova, and relations to hæmal and perihæmal systems see 6, pp. 184-5, and 7, pp. 4-9.)

The season of ripeness in the Firth of Clyde lasts from about the beginning of March to the end of the first week in April. Each starfish may spawn several times during this period, at intervals of two to ten days. The presence of other spawning individuals acts as a stimulant, and "epidemics" of spawning occur in tanks containing numerous starfish. A full-sized female may shed more than two thousand ova at a time, and probably more than six thousand altogether. The brooding habit is absent. There is no invariable spawning position. Commonly, however, spawning starfish will be found bunched up under water and adherent only by the outer portions of their rays, or else right at the surface with half of the disc and arms detached and extended outwards. Occasionally they may be observed spawning in the ordinary extended position, motionless under the water.

The ova, which are a little smaller than those of *S. endeca*, measure about .8 mm. in diameter, being rather wider in

equatorial than in vertical measurement. They float, the lower pole being rather lighter in weight and paler in colour than the upper one. There is more variety of colour than in the case of *S. endeca*, the general tint in ova from different starfish varying from reddish-orange to terra-cotta or clay. The polar bodies emerge from the middle of the upper pole. Maturation is in progress as the eggs are being shed and fertilisation is followed by formation of a membrane of fertilisation.

Segmentation is total and equal, the first two cleavages being vertical and at right angles to one another, while the third is equatorial. Continued cleavage produces a practically solid mass of small cells of which more than a hundred can be counted in a single section. Blastula formation takes place by egression (see Masterman, 19, p. 380) of the more centrally placed cells along lines which show up as grooves on the surface. During this process the cell walls disappear in great part, except just at the surface, so that the interior is almost a syncytium. The egression grooves are at first numerous, and their arrangement recalls that of the surface furrows in the later segmentation stages. Gradually the grooves become fewer and simpler until resemblance to a sixteen-celled, an eight-celled, a four-celled, or even a two-celled stage is reached. The solid morula is now converted into a hollow single-layered blastula. Its wall increases in thickness as the folds smooth out, only losing the last of these as gastrulation proceeds.

Gastrulation begins in the middle of the under-surface, to all appearance by deepening of an egression groove in this region, or of two such grooves crossing one another. The gastrula opening is therefore at first usually elongated, but sometimes cruciform, or tri-radiate. As the involution deepens, all other superficial markings are smoothed out, and the gastrula opening becomes circular. The transition between the paler cells of the under-pole of the egg and the more highly-coloured cells of the upper pole is to be found a short distance out from the lip of the blastopore all round. The

gastrula is now somewhat flattened on the under side, its vertical being a little less than its equatorial diameter.

Cilia appear on the surface during blastula formation while the egg is still enclosed within the membrane of fertilisation. This membrane becomes lost about the time when gastrulation begins. The young gastrulæ swarm slowly about, at first somewhat irregularly, but afterwards rotating on their vertical axes with slight epicyclic progression in a direction corresponding with the rotation. The rotation may be dextral or sinistral as viewed from above, and not infrequently reverses itself. In section the gastrula is found to be two-layered, each layer being made up of elongated columnar cells with cilia on their free surfaces. During blastula formation, yolk-granules are often extruded from the surface, and a quantity of these may be swept into the archenteron, which, however, at this stage is otherwise empty as a rule, the formation of "hypenchyme" being either absent altogether or very much less well-marked than has been described by Masterman in the case of *Cribrella* (19).

EXTERNAL CHANGES UP TO AND AFTER FIXATION.

Early Larva up to Fixation.—The gastrula elongates to about twice its former vertical measurement, the middle of the upper surface becoming the anterior extremity of the larva. A depression forms on what will be the ventral side of the larva near the junction of its second and third fifths. Rudiments of the three brachia then grow out, one in front of and the other two to right and left of, and slightly behind, the middle of this depression, where the rudiment of the sucker now appears. The portion of the larva which carries the brachia and the sucker may be called the præoral lobe. The posterior portion or body of the larva has meantime become flattened out in the sagittal plane, and the blastopore has gradually become smaller. As a rule it still retains its original position in the centre of the posterior end of the larva, although in a good many cases it becomes pressed

slightly ventrally and to the right owing to prominence of its left dorsal margin. Otherwise the larvæ exhibit till now perfect bilateral symmetry.

A shallow ectodermal depression, at the bottom of which the hydroporic opening forms, appears on the right side of the body of the larva anteriorly some distance from the dorsal edge. The next important features to be noted are closure of the blastoporic opening, increase in length of the brachia, greater prominence of the sucker, sharper division of the larva into præoral lobe and body, the last-named portion becoming more disc-like through flattening from side to side.

As regards movements, at first the larvæ, being still rather lighter than water, remain in a vertical or slanting position with the anterior end uppermost, rotating clockwise as viewed from the anterior end, and progressing slowly with this end in advance. Reversals of the direction of rotation and progression may occur for short periods. Later, the larvæ (Pl. 10, figs. 1-4), becoming relatively heavier, rise or sink in the water, according to the activity of their ciliary action. The brachia now show movements of shortening and lengthening, closing together, and divarication. Their ends are glandular and slightly adhesive, enabling the larva to attach itself loosely to smooth surfaces.

Fixation by the sucker occurs about the nineteenth day. The larvæ take first hold by the tips of the brachia, which then become widely separated and shortened by muscular action, while at the same time the sucker is pushed out. The sucker adheres at first by muscular action, but afterwards by throwing out a thin layer of cement. A very important external change is occurring, namely, flexion and torsion of the præoral lobe on the body or disc, with the left side of which this lobe becomes gradually incorporated (Pl. 10, figs. 5-7). The flexion is a leftward one, and when completed may be counted as being through two right angles, since it ultimately flattens out the anterior end of the larva on the left side of the disc. The torsion takes place dextrally as viewed from the anterior end of the larva, through an

angle of 75° or thereby. The hydrocœle lobes appear externally as swellings very shortly after fixation has been effected (Pl. 10, fig. 6). Lobes III and IV usually show up first, then II and V, then VI, and lastly I. This is slightly different from the sequence in which the radial pouches first make their appearance internally on the wall of the hydrocœle (see p. 163).

The flexion and torsion of the præoral lobe produce a marked notch on the margin of the disc in the junctional region on its (larval) dorsal side. This is the so-called aboral brachiolarian notch. It afterwards becomes gradually filled out, forming interradius I/II—the madreporic inter-radius. Shallow indentations also appear on the margin of the disc, indicating succeeding interradii, namely, II/III to V/VI. There is still a segment of the disc between V/VI and I/II, amounting to rather less than a third of a circle, which has as yet no notches, but in which the remaining armrudiments will afterwards form.

Hydrocœle lobe VII next appears beyond VI, on the sinistral¹ side of the latter, and much further back in differentiation. The next lobe to become evident is XII, which arises close to I, and on its dextral¹ side. Lobe VIII now makes its appearance sinistral to VII, and shortly thereafter XI dextral to XII. Lobe IX (sinistral to VIII) is the next to show up, and X the last in the small interspace still intervening between IX and XI. Meantime the general mass of the præoral lobe, as well as the brachia, and finally, the sucker, have been disappearing, and the last remains of the sucker are to be found opposite lobe X or in interradius IX/X, just outside the completed hydrocœle ring (Pl. 10, figs. 8-9). At the time of their first appearance the hydrocœle lobes are blunt swellings; then they become trilobate through differentiation of the proximal pair of sucker feet and of the terminal tentacle. Succeeding pairs of sucker feet appear between the terminal tentacle and the latest formed pair. About the twenty-eighth day the proximal pairs of sucker feet

¹ See footnote on p. 156.

on the first six hydrocœle lobes begin to be functional. The young starfish may now shift position while still remaining anchored by the sucker, the stalk of which can stretch out a length of over 1 mm. Similar movements occur at a corresponding stage in the case of *A. rubens*, but whereas in the latter starfish the sucker ultimately separates off and is left behind, in *Solaster* this structure, after becoming smaller, loosens its hold, and is absorbed. The loosening usually takes place before lobes IX, X and XI have become clearly marked out. In the course of further growth the formation of interradial notches between the later-formed rays is gradually effected. Notches VI/VII and VII/VIII appear first, then XII/I, the remaining notches, viz. VIII/IX, XI/X and IX/X being the last to appear. By this time notch I/II, i. e. the brachiolarian notch, has filled out so that it is no deeper than the rest. It will be remembered that arm-rudiment I is formed from the (larval) ventral lip of the notch in question.

Slight prominences containing developing spines begin to appear about the twenty-second day all over the aboral surface, including the interradial notches and the sides of the aboral arm-rudiments (see under "Skeleton," p. 178). The spines develop latest on the part of the disc where the last formed arm rudiments are gradually becoming marked out (Pl. 10, fig. 8).

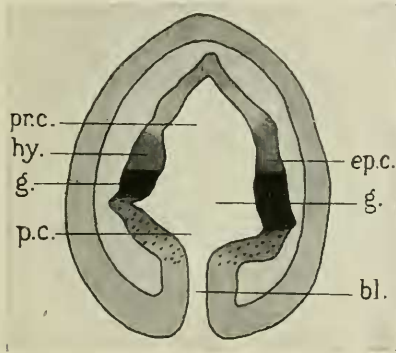
The mouth appears about the thirty-eighth day, characteristically in the form of a tri-radiate fissure, the angles of which point more or less directly towards interradial notches XII/I, III/IV, and VII/VIII (Pl. 10, fig. 9). The anus appears much later—about the end of the seventh week.

DEVELOPMENT OF CAVITIES AND ORGANS.

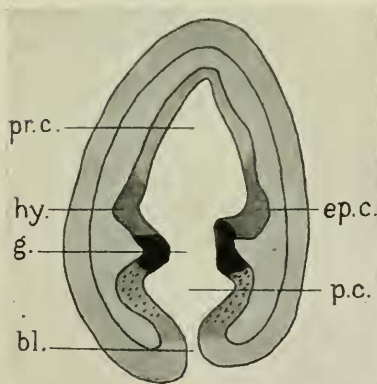
At first the archenteron follows the shape of the elongating larva, but about the seventh day begins to show constrictions marking off (a) anterior, (b) middle and (a) posterior regions, without there being any indication of such a division on the

external surface of the larva (Text-figs. 1-4). These regions are respectively (a) the anterior larval cœlomic cavity, (b) the enteron, and (c) the posterior larval cœlomic cavity,

TEXT-FIG. 1.



TEXT-FIG. 2.



TEXT-FIGS. 1-2.—See explanation on p. 165.

and it will be now convenient to follow out the development of each, noting meantime that mesenchyme arises abundantly at this stage by budding from the walls of the anterior and posterior cavities, but chiefly of the latter.

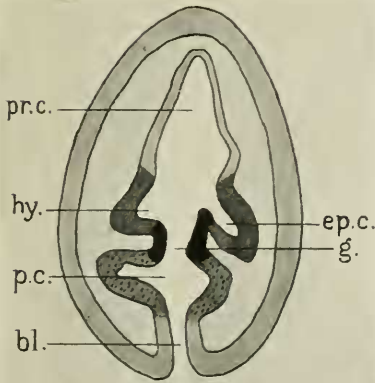
Anterior Larval Cœlomic Cavity.—This cavity extends (1) into the præoral lobe and the brachia and (2) backwards to right and left of the enteron, forming right and left lateral diverticula, and it also sends from its postero-dorsal portion a pocket to the right, which becomes the hydroporic canal, the inner end of the latter being, to begin with, approximately in the middle line. The outer end of this canal meets and fuses with the bottom of a slight pit on the right side of the larva dorsally, giving rise to the hydroporic opening. The following derivatives of the anterior larval cœlomic cavity now fall to be described: cavity of præoral lobe, hydrocœle, epigastric cœlom, axial sinus, axial organ, stone-canal, and internal oral circular sinus.

Cavity of Præoral Lobe.—The cavity of the præoral lobe gets obliterated as the lobe itself is reduced. The attaching stalk has become solid by the time the ring-canal of the hydrocœle is completed, and accordingly we cannot say that the hydrocœle ever encircles the stalk-cavity. However, the central portion of the anterior cœlom from which the stalk-cavity came off is still relatively large at the stage we are considering, and lies within the circle of the completed hydrocœle ring.

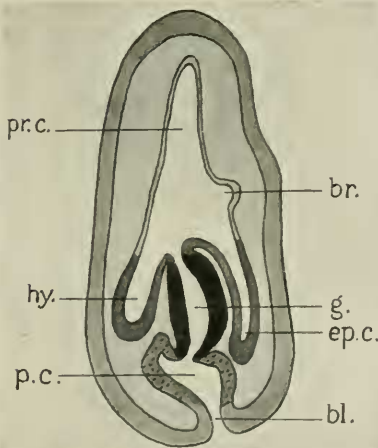
Hydrocœle.—The hydrocœle pouches appear as out-pocketings of the left lateral diverticulum of the anterior cœlom. Pouches I–V are formed at much the same time, I being, perhaps, a little delayed; VI comes immediately thereafter sinistral¹ to V; then, more slowly, VII sinistral to VI; then XII dextral¹ to I; then VIII sinistral to VII; then XI dextral to XII; then IX sinistral to VIII; and finally X in the interspace remaining between XI and IX. It will be remembered from p. 161 that the external swelling for pouch I was relatively somewhat later in appearing, probably owing to the imprisonment of this swelling in the corner to which the præoral structures are being retracted. The hydrocœle ring-canal gets nipped off from the bottom of the left lateral diverticulum earliest in the

¹ See footnote on p. 156.

TEXT-FIG. 3.



TEXT-FIG. 4.



Text-figs. 1-4.—Optical sections of *Crossaster* larvæ (7-8 days), to illustrate subdivision of archenteron into gut and primary larval cæломic cavities. The smaller size of the left wall of the enteric isthmus will be noted all through, and at stage shown in Text-fig. 4 a greater backward extension of the epigastric cælom than of the hydrocæle. *bl.* Blastopore. *br.* Cavity of an out-growing lateral brachium. *ep. c.* Epigastric cælom. *g.* Enteron. *hy.* Hydrocæle. *p. c.* Posterior cælom. *pr. c.* Preoral cælom.

region of pouches II-IV. This canal is at first crescent-shaped and open at either end, but shortly after fixation, by extension of the nipping-off process, its dorsal and ventral horns end blindly. The blind ends have now to push their way round from either side so as to meet, and by uniting complete the hydrocœle ring. The completion takes place in interradius IX/X, rather nearer X than IX. Pouches VI to IX have arisen from the ventral horn of the hydrocœle crescent and pouches XII-X from the dorsal horn. At first the hydrocœle crescent is a segment of a relatively small circle. Later, the area enclosed becomes much larger through incorporation of præoral lobe epiderm with the body in this region. This increase in size provides room for the formation of the mouth. The sucker and the brachia disappear by histolytic absorption.

Epigastric Cœlom.—The right lateral diverticulum of the anterior larval cœlomic cavity becomes cut off by constriction from the præoral cœlom, and since it gives rise to the adult epigastric cœlom is to be looked on as equivalent to a right posterior cœlom (*Asterina* (13), *Asterias rubens* (7), *Porania* (9), and cf. p. 180). The constriction is a result of (1) the flexion and torsion of præoral lobe already described, and (2) the growth of the dorsal and ventral horns of the posterior cœlom (p. 174). The intestine and rectum grow up (sixth week) as an aboral-ward pouch between the layers of the mesentery separating the epigastric from the hypogastric cœloms in interradius V/VI near the middle of the aboral surface. This mesentery afterwards becomes broken up to form the aboral ligaments of the stomach. A bilobed pouch from the epigastric cœlom extends outwards in each ray above the developing radial cœca (p. 177), its walls forming the aboral or suspensory ligaments of these cœca.

Axial Sinus.—The axial sinus is the remains of the central portion of the anterior cœlomic cavity after (1) the præoral lobe portion disappears, (2) the hydrocœle ring-canal is nipped off from the left lateral diverticulum, and (3) the internal oral perihæmal ring is (see below) reduced to its

proper size. The hydroporic canal now opens internally to the right or aboral side of the former larval sagittal plane.

Stone-canal.—As in *Solaster endeca*, the stone-canal appears to be formed partly as an outgrowth from the hydrocœle groove in interradius I/II and partly as a furrow in the wall of the axial sinus. Furrow and outgrowth establish continuity with one another and the furrow becomes roofed in except at its aboral extremity near the internal opening of the hydroporic canal, where it opens into the axial sinus. For an account of the later development and adult structure of the pore-canal system and madreporite see (8).

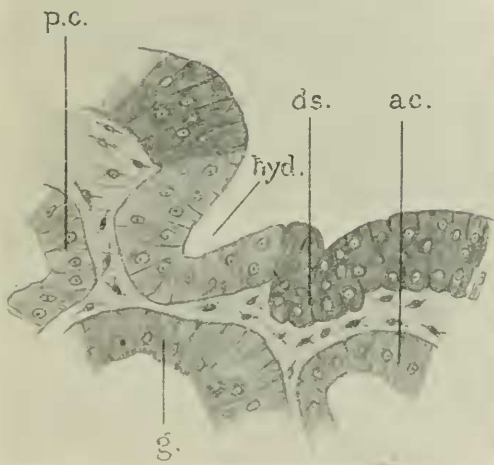
Axial Organ.—The axial organ begins during early metamorphosis as a cell thickening, soon rising into a fold, of the wall of the axial sinus, commencing below the madreporic vesicle and continued orally into a somewhat prominent crescent of spongy tissue in the still spacious (see below) portion of the internal oral perihæmal ring opposite the stalk. (This crescent, afterwards becoming smaller and extending round the mouth, forms the oral hæmal ring.) The fold of the axial organ contains (1) spongy channels continuous with those which are being invaginated from below into the madreporic vesicle (p. 163); (2) cells derived from the lining of the axial sinus; (3) cells derived from the floor of the madreporic vesicle and its oral-ward pocket, some connected with fibres running chiefly in the longitudinal axis of the fold. A little later than (1) and (2) the dorsal horn of the posterior cœlom provides a well-marked ingrowth (of primitive germ-cells—MacBride, *Asterina*, *Amphipura*, etc.) just below the madreporic vesicle.

Internal Oral Perihæmal Ring.—This ring (internal oral circular sinus) is a derivative of the central portion of the anterior larval cœlomic cavity and of that portion of the left lateral diverticulum which remains after the hydrocœle canal is nipped off. In the formation of the mouth, epiblast and hypoblast become continuous across these remainders, which are not, however, entirely obliterated. What is left of them lies around the mouth and forms the internal oral sinus,

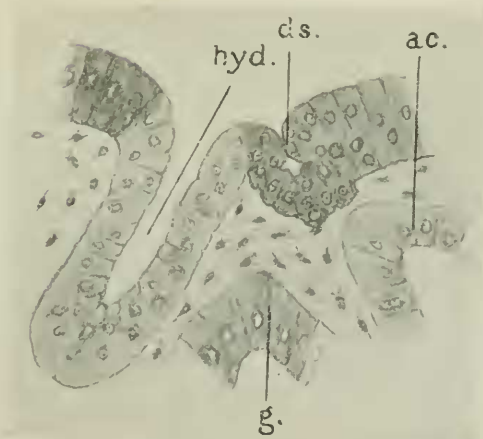
being spacious at first in the region of the stalk, but for a time obliterated just opposite to that region, so that we can describe the sinus in question as being in a sense completed by outgrowth from the axial sinus. In the adult, as in the larva, it communicates with the axial sinus.

Dorsal Sac or Madreporic Vesicle (see also p. 181). —Contrary to all expectation the madreporic vesicle has been found to arise from epiblast (Text-figs. 5-6), sometimes as a solid ingrowth of cells, afterwards becoming separated off and acquiring a lumen, and sometimes by the formation of a pit, the bottom of which gradually becomes constricted off from its parent surface (Text-figs. 7-8). Its place of origin is immediately ventral to the hydroporic opening, and close to the junction of the epiblast with the enterocœlic wall of the hydroporic canal. Normally it begins to form just after the hydroporic opening has been established, but its rudiment is sometimes recognisable prior to this event. At first the vesicle wall is made up of columnar or cubical cells. These afterwards become flattened. Towards the end of metamorphosis the madreporic vesicle is found to have sent down a rather long, narrow oral-ward pocket into the upper end of the axial organ. Beneath the vesicle on the side looking towards the pore-canal a vacuolated space appears (thirteen to sixteen days) in the mesenchyme. Prior to metamorphosis this space can be recognised as extending (Text-fig. 10) at one part into the tissue of the future aboral body-wall, and at another over the aboral wall of the stomach, while a later extension can be noted down the wall of the axial sinus in the line of the developing axial organ. The main space is spongy, being traversed by fibrillæ, and the spongy tissue is invaginated at metamorphosis into the madreporic vesicle, forming the so-called head-process of the axial organ, which appears to be homologous with the "heart" of *Balanoglossus*. Tissue opacity precludes observations on the question of pulsation in the larva, but a dissected-out "heart" in the adult shows faint sub-rhythmic contractions (8, p. 272). In later growth the invagination of the "heart"

TEXT-FIG. 5.

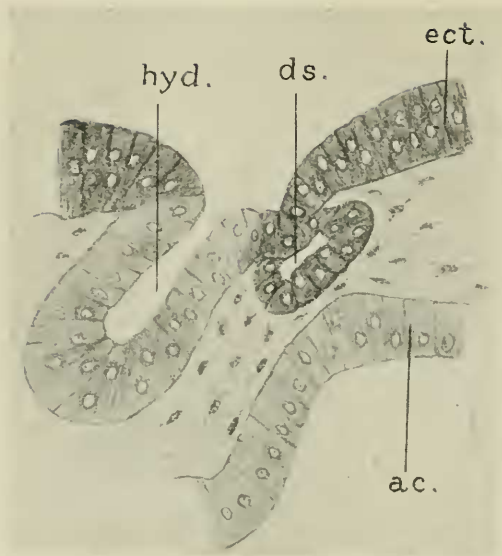


TEXT-FIG. 6.



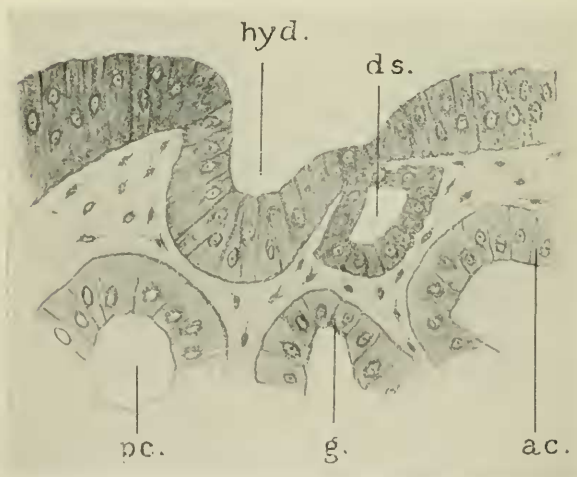
Text-figs. 5-6.—Sections across hydroporic region of *Crossaster* larvæ, 12 days old, drawn as viewed from posterior end of larvæ. The layers and nuclei were mapped out with the camera lucida. At this stage the dorsal sac is a thickening or an involution of epiblast immediately ventral to the junction of the latter with the wall of the hydroporic canal. *ac.* Anterior cœlom. *ds.* Dorsal sac. *g.* Enteron. *hyd.* Hydroporic canal. *pc.* Posterior cœlom.

TEXT-FIG. 7.



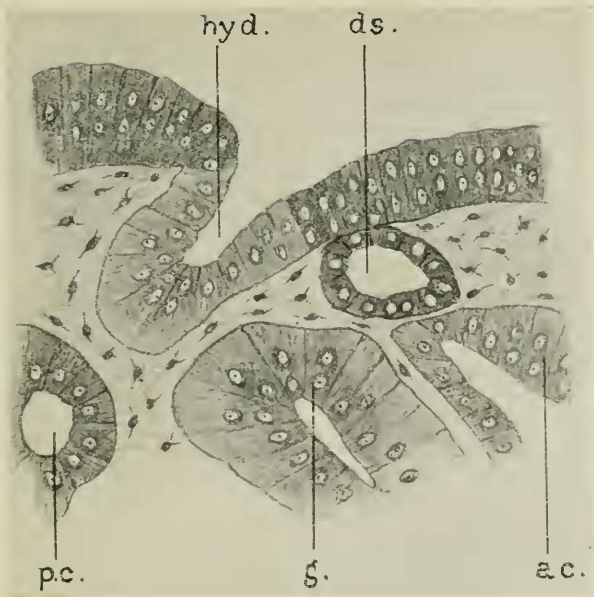
The dorsal sac is becoming constricted off from the epiblast and has a minute lumen. (See under Text-figs. 5-6, p. 169.)

TEXT-FIG. 8.



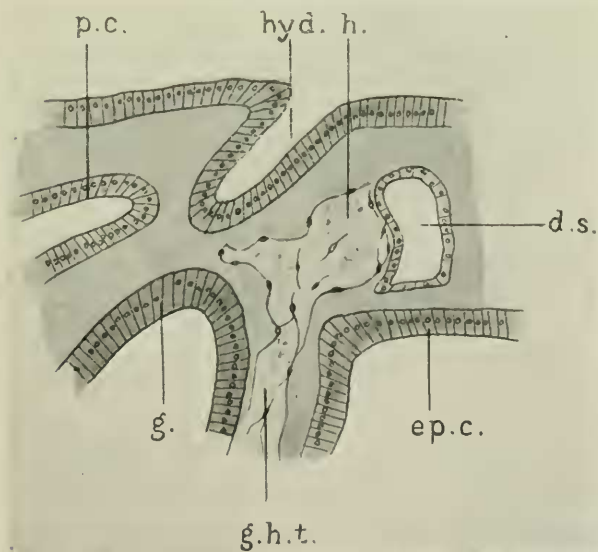
The sac is increasing in size (13-14 days) and is almost completely separated off from the epiblast, the surface of which, as in Text-fig. 7, still shows a slight dimple marking where the involution of the sac first took place. (See under Text-figs. 5-6, p. 169.)

TEXT-FIG. 9.



The sac is now (15 days) completely separated off from the epiblast, but is still relatively thick-walled. (See under Text-figs. 5-6, p. 169.)

TEXT-FIG. 10 (semi-diagrammatic).



The sac has now migrated deeper (16-17 days), is thinner-walled, and shows beside it a spongy space, the future "heart" (*h*), channels from which are seen extending on the future aboral aspect of the gut-wall. (See under Text-figs. 5-6, p. 169.)

into the madreporic vesicle can be recognised as being along a line, at the two extremities of which are the communications of the "heart" respectively (1) with the body of the axial organ, and (2) with the aboral body-wall spaces, the former being on the deep side axially and the latter on the superficial side. The two extremities retain their proper connections, but the portion between them loses its attaching mesentery ("mesocardium") within the madreporic vesicle, as occurs in the case of a developing vertebrate heart-tube within the pericardial cavity.

The relations of the central portions of the hæmal system are illustrated in Text-figs. 11-12, and reference may be made for further details and for a comparison with the hæmal system of *Balanoglossus* to 8, pp. 271 and 278, and to 'Quart. Journ. Micr. Sci.,' 1919, p. 537. Reasons are there given for instituting a homology between the axial organ in Echinoderms and the left collar vessel and the left part of the glomerulus in *Balanoglossus*. The vessel in question is a rete mirabile (Spengel, 25, p. 753), which lies within a fold of the left collar cœlomic wall.

Madreporite.—The relations of pore-canals, axial sinus, etc., in the adult madreporites of *Asterias rubens* (8) and *Solaster endeca* (6) have already been described by the author. In the last-named star-fish the ampulla of the "stone-canal" is represented by a sac with thick glandular walls completely invaginated into the madreporic vesicle, and connected by a long, narrow neck with the collecting spaces of the pore-canal system. Light is thrown on the development of such an ampulla by intermediate *Crossaster* growth stages where (e. g. in specimens from $\frac{1}{2}$ in. to 1 in. across) the ampulla is a thick-walled wide-necked cavity bulging into the madreporic vesicle (Text-fig. 12). In *Asterias rubens* the ampulla is relatively large and lies directly over the madreporic vesicle, from which it is separated by a thin membrane.

The ampulla has probably a hydrostatic function (8, p. 272), and permits changes of volume on the part of the "heart"

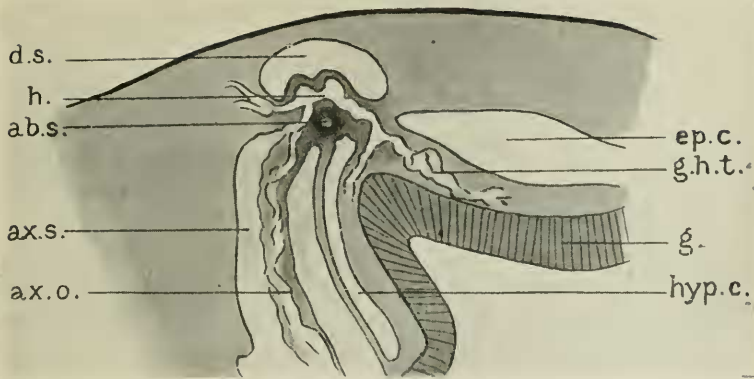


Diagram illustrating relations of heart towards end of metamorphosis, showing its communications (the future gastric hamal tufts) with the stomach-wall, and also with the axial organ and the aboral body-wall. (See under Text-fig. 12.)

TEXT-FIG. 12.

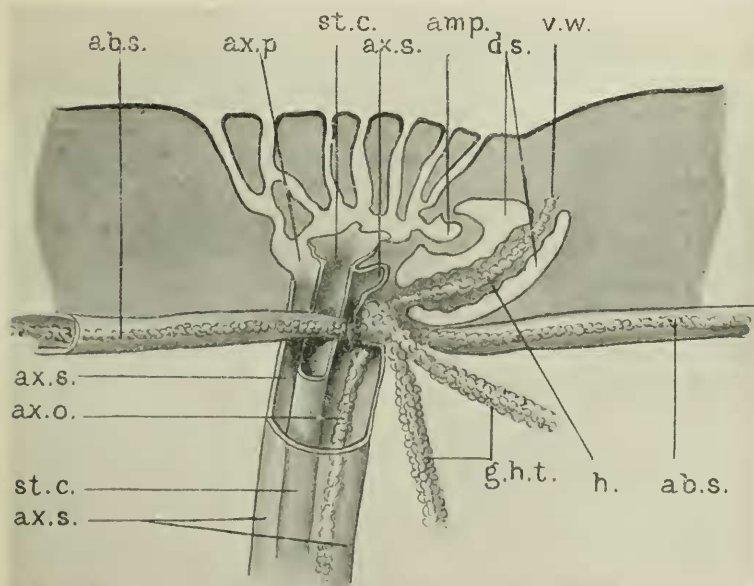


Diagram to illustrate relations of pore-canal system, axial sinus, etc., madreporic vesicle, "heart," and principal hamal vessels in a young *Crossaster*, 25 mm. across the disc (see p. 172). The madreporite, the madreporic vesicle, the ampulla, and the upper parts of the stone-canal and axial sinus are seen in vertical section as from somewhere near the centre of the disc. *ab. s.* Aboral sinus. *amp.* Ampulla of stone-canal. *ax. o.* Axial organ. *ax. p.* Main opening of axial sinus into pore-canal system. *ax. s.* Axial sinus. *ds.* Dorsal sac or madreporic vesicle. *g.h.t.* Gastric hamal tufts. *h.* "Heart." *st. c.* Stone-canal. *v. w.* Communication of "heart" with spaces in aboral body-wall.

(head-process of axial organ) within the madreporic vesicle, this vesicle being surrounded by rigid tissue except where it abuts against the ampulla.

The Larval Posterior Cœlomic Cavity.—When first recognisable this cœlom is a rounded cavity, which sometimes lies symmetrically at the posterior end of the larva, but sometimes appears swollen dorsally and to the left, causing the prominence of the left dorsal part of the blastoporic lip referred to on p. 159. As the body of the larva becomes flattened laterally the posterior cœlom grows out dorsally and ventrally, giving rise to dorsal and ventral horns, the former of which at first keeps slightly to the left of the middle line. The dorsal horn grows forward till it is arrested by the axial sinus portion of the anterior cœlom. At this stage it often shows bifidity, the left tip being destined to form perihæmal pouch I/II, and the right one pharyngeal pocket I/II and the cœlom within arm-rudiment II. The ventral horn extends first in a forward and then in a dorsal direction until it also is arrested by the anterior cœlom. The tip of this horn lies in the ventral lip of the aboral brachiolarian notch, and when the notch in question becomes reduced to form interradius I/II, gives rise to the cœlom within arm-rudiment I. Accordingly, while hydrocœle pouch I is derived from the larval dorsal, arm-rudiment I is derived from the larval ventral side of the brachiolarian notch. In its growth forward the ventral horn passes slightly to the right of the middle line and its tip also sometimes shows temporary bifidity. The principal derivatives of the posterior cœlom are the hypogastric cœlom, the pharyngeal or perioral cœlom, the external oral perihæmal pockets, the genital rachis, and the aboral perihæmal sinus.

Hypogastric Cœlomic Cavity.—This large cavity is derived wholly from the posterior cœlom and its dorsal and ventral horns. During and after metamorphosis it extends orally and aborally, thus covering a portion of the enteron both on the oral and aboral sides. The layers between it and the epigastric cœlom form the circular epigastric mesentery,

which ultimately becomes broken up into ligamentous strands except above the radial cæca. Outgrowths from the main cavity give rise to the cavities within the arm-rudiments, that of arm-rudiment II being derived from the tip of the dorsal, and that of arm-rudiment I from the tip of the ventral horn. During, and for some time after, metamorphosis, the dorsal and ventral horns are separated by the axial sinus, which abuts against the enteron wall. Later, however, the two horns communicate freely between axial sinus and enteron wall, owing chiefly to extension of the dorsal horn in this region. The two gastric hæmal strands are specialised bands belonging to the series derived from the circular epigastric mesentery (p. 166).

Perioral or Pharyngeal Cœlom.—This cœlom arises in the form of pockets from the posterior cœlom, coming off internal to the hydrocœle ring, and pushing into the tissue between this ring and the gut. Pockets III/IV and IV/V arise earliest, then II/III, V/VI, VI/VII, XII/I, I/II, VII/VIII, XII/XI, VIII/IX, XI/X, and IX/X. The first-formed pockets (I–VI) are completely separated off at a stage when the later ones (VIII/IX and X/XI) are in course of formation and the last one (IX/I) has not yet appeared. Pouch I II arises from near the tip of the dorsal, and pouch XII/I from near the tip of the ventral horn; after their separation the pockets extend towards one another, and ultimately fuse to form a continuous cavity round the position of the future mouth. Their stalks of origin become obliterated with the exception that the first of them, i.e. that in interradius I/II, does not appear to close. When the fusion of the pockets is complete, the resulting pharyngeal cavity is separated from the main hypogastric cavity by a circular mesentery, except in interradius I/II. This sheet becomes perforated first interradially and then radially, giving rise to the various ligaments connecting the oral aspect of the stomach with the body-wall.

External Oral Perihæmal Ring.—This ring arises in the form of interradiial pockets, all of which take origin from

the posterior cœlom, and, growing out external to the hydrocœle ring, interdigitate with the hydrocœle pouches. They appear several days later than the pouches between which they lie and in similar sequence. Thus, those in interradii I/II to V/VI appear practically together, III/IV and IV/V being a little in advance. Then in order come VI/VII, XII/I, VII/VIII, XII/XI, VIII/IX, X/XI and IX/X, as in the case of the pockets for the pharyngeal cœlom. I/II, II/III, etc., arise from the dorsal horn, and XII/I, XI/XII, etc., from the ventral horn of the posterior cœlom. As the radial canals of the hydrocœle grow out, each perihæmal pocket sends a prolongation along the adjacent sides of the two radial canals bounding the interradius in which it lies, as MacBride first pointed out in the case of *Asterina* (13, p. 560). As in *Solaster* (6, p. 188) and *Asterias* (8, p. 260) each pocket also sends an interradiial branch aborally into the tissue of the interbrachial septum.

Genital Rachis and Aboral Perihæmal Ring.—So far as I can make out the development of these two structures occurs in the manner described by MacBride for *Asterina* (13), viz. by the formation of a pocket pushing out from the dorsal horn of the posterior cœlom just below the madreporic vesicle, and afterwards extending horizontally round the disc and sending two branches outwards in each interradius. I do not find, however, that there is a growth of recognisable germ-cells down the length of the axial organ.

The Larval Middle Cavity or Enteron.—At first the enteron is simply an isthmus between the anterior and posterior cœloms, compressed from side to side so as to form a short slit-like passage. The dorsal extremity of the slit is a little to the left of the middle line and the ventral extremity a little to the right. The right wall of the slit is rather larger than the left and is slightly pouched to the right. The opening between the enteron and the posterior cœlom becomes closed about the eighth day, its last traces being found nearer the ventral than the dorsal end of the slit and looking slightly to the right. The opening between enteron

and anterior cœlom does not close till a day or two later. The last trace of this opening is found near the dorsal end of the slit, and looks leftward owing to the greater size and prominence of the right enteron wall in this region. After separation the enteron expands slowly, becoming, in the first place, bluntly gibbous in shape, with dorsal and ventral horns which fit within the crescent formed by the posterior or hypogastric cœlom. During metamorphosis it increases in size and thickness, and a very active transference of yolk-granules from the other tissues, particularly from the parts undergoing reduction, takes place into the cells forming its walls, which for a time become syncytial. Blunt expansions next appear opposite the rays, and these will be recognisable afterwards as the radial dilations of the gastric portion of the stomach. At the same time a pyloric sac region becomes marked out aborally, and from this sac the pyloric or radial cœca begin to grow outwards. Both kinds of outgrowths appear first in the earliest-formed rays, and subsequently in the other rays, according to the sequence in which these became differentiated. We have to note that the cœca for ray I arise from what was the ventral horn of the gut during its former gibbous stage.

The œsophagus takes origin (sixth to seventh week) on the (larval left) adult actinal aspect, as an outgrowth of the enteron which bridges the central part of the anterior cœlom and the remains of the left lateral diverticulum of this cœlom, and fuses with the left body-wall in the middle of the area enclosed by the hydrocœle crescent. The contingent layers become reduced and then absorbed. There is no stomodæal invagination. Usually, though not always, the mouth opening is at first tri-radiate, the angles pointing more or less in the direction of rays III/IV, VII/VIII, and XI/XII.

The intestine takes origin excentrically in interradius V/VI as an outgrowth from the roof of the pyloric sac between the layers of the circular epigastric mesentery. The outgrowth expands at its extremity to form the rectal sac, which projects chiefly into the hypogastric cœlom. The rectum grows out

from this sac in interradius V/VI (see 6, p. 180), continuing the line of the intestine. It gradually burrows through the aboral body-wall in the same inter-radius, and meeting with a shallow depression from outside forms the anus, which, however, is unprovided with a proctodæum.

SKELETON.

The aboral skeletal plates arise as in *Solaster endeca* (7, p. 41) in the form of scattered calcifications, without definite radial or inter-radial arrangement, except that groups of two or more are recognisable from an early stage in the position of the future terminals. As the disc increases in size, additional calcifications appear between the original ones. In the end the earlier-formed plates become nodal points in the skeletal reticulum, and each develops on its superficial aspect a rounded boss or hump for the support of a group of spines. An important point to note is that in each ray the adult terminal arises by the fusion of several (usually five) originally separate calcifications placed at the tip and just at the sides of the tip of the ray. The same process occurs in *Solaster endeca* (7) and in *Cribrella* (10). So far as I know, this is the first ascertained instance among Echinoderms in which a primary skeletal plate takes origin by the union of earlier scattered calcifications. It is altogether likely that in primitive Echinoderms the skeletal plates were numerous, small, and without definite arrangement, and we are probably justified in inferring that the primary plates which appear radially and interradially in the development of such starfish as *Asterina gibbosa* and *Asterias rubens* are the ontogenetic representatives of groups of ancestral plates. This circumstance may help us to realise how far any particular form must have travelled towards specialisation by the time it exhibits quinque-radiate symmetry in the ontogeny of its skeletal plates.

The spines arise as calcifications in the superficial layer of the dermis, and are at first numerous and uniformly distributed over the abactinal surface, except that they appear

latest in the region of the last-formed rays. We next find them set singly, or in groups of twos or threes—the first *paxillæ*—over the larger skeletal plates.

The development of the ambulacral and adambulacral plates follows the course described by Ludwig in *Asterina* (12) and by the author in *Solaster endeca*, the first ambulacrals being proximal to the first tube-feet in each ray, and the first adambulacrals forming the mouth-angle plates. However, from careful maceration experiments, it appears that each first ambulacral is continuous in origin and early growth with the corresponding first adambulacral or mouth-angle plate, the joint which finally separates them being of secondary formation. This is interesting in view of the fact that palæozoic Asterozoa (Spencer, 24, p. 30), have no ambulacral plates proximal to the first tube-feet. We may infer that the first ambulacrals of recent starfish are new formations, and that they have arisen as buttress extensions from mouth-angle plates towards the middle of each ray. This will throw light on the distinction between the adambulacral and the ambulacral types of mouth-armature in recent starfishes, the former being presumably the more primitive.

In any case, two important facts have been established regarding particular "primary" plates: (1) That in the terminals we have an example of fusion of previously-formed calcifications, and (2) that in the first ambulacrals the converse process, namely, separation from a larger calcification, is exemplified.

GENERAL.

Among features of general interest in the foregoing which claim further notice are the following: (a) The mode of origin of the *cœloms*; (b) the mode of formation of the dorsal sac or madreporic vesicle; (c) the origin of the pharyngeal or perioral *cœlom*; (d) the origin of pocket I/II of the external oral perihæmal ring; (e) the sequence in the formation of the hydrocœle pouches; (f) the relation of the larval stalk and sucker to the hydrocœle ring; (g) peculiarities in the development of the skeleton (see above).

(a) Origin of Cœloms.—Neither in *Solaster endeca* (7) nor in *Crossaster papposus* is there any indication of an origin of the posterior cœlom by constriction from the anterior cœlom, and the gut is an isthmus, not a diverticulum of the archenteron. In *Asterias rubens* (8), *A. glacialis* (10) and *Porania pulvillus* (9) I described rudiments of an independent posterior cœlomic outgrowth from the enteron. In Enteropneusts, Morgan (20, p. 413) and Bateson (1) have ascribed a posterior origin to the trunk cœloms, while Davis states that these arise through backward growth of the anterior cœlomic sacs. In *Asterias rubens* (7), as in *Asterina* (12), the hypogastric cœlom of the adult is derived entirely from the larval left posterior cœlom. I have accordingly put forward (8, p. 234) the view that in Enteropneusts and Echinoderms generally there are two potential modes of origin of the posterior cœloms: (1) by constriction from an anterior cœlomic outgrowth, and (2) by a separate posterior outgrowth from the enteron. As regards *Crossaster* and *Solaster*, the conclusion is drawn that both modes of origin are represented, the former on the right side of the larva and the latter on the left side. Thus on the right side the epigastric cœlom takes origin as a backward diverticulum of the anterior cœlom, while on the left side the hypogastric cœlom arises independently behind the enteron. In this connection it will be remembered that actually at any early stage the right lateral diverticulum of the anterior cœlom extends further back than the left diverticulum (Text-fig. 4), while the posterior cœlom has frequently its greatest extension dorsally, and to the left. (See also discussion in 8, p. 234.)

(b) Dorsal Sac.—It was a great surprise to find that in *Crossaster* and *Solaster* the dorsal sac takes origin from the epiderm. I hesitated to publish this result until I had obtained and examined sets of ova from three separate spawnings. MacBride and Masterman state that the sac in question has a cœlomic origin in *Asterina* (13) and *Cribrella* (19) respectively. I had recently the opportunity (1916) of verifying this statement beyond the possibility of

doubting in the case of *Cribrella* from reared larvæ. As regards *Solaster endeca*, when I worked out its development (1910) the evidence was not at first conclusive, but later some of my material showed the sac arising from the anterior cœlom, and accordingly I stated (7, p. 26, 1912) that, so far as I could make out, the dorsal sac is budded off from the anterior cœlom. But unfortunately this later material had been supplemented by plankton-gathered larvæ (19), and along with these a few *Cribrella* larvæ prove to have been collected, and to have been mistaken, most regrettedly, for *Solaster*. At that time it had not been put on record, as I have since done (10), that *Cribrella* eggs may be pelagic, a brooding habit being stated to be characteristic of the species (19). The two species have the same spawning period, and their eggs and larvæ resemble one another during early stages, and although the anterior brachium normally remains single in *Solaster* and becomes double in *Cribrella*, still it is occasionally doubled in the former.

I cannot suggest any satisfactory explanation which will reconcile the epidermal origin of the sac in *Crossaster* and its cœlomic origin in *Asterina* and *Cribrella*, etc., and its apparently mesenchymatous origin in certain other forms. Possibly the re-arrangement of the central cells during blastula formation may provide opportunity for portions of tissue from deeper layers being lined up thus early with the epiblast. Or, again, in larvæ like that of Echinoderms, it is by no means inherently out of the question that the formative tissue of a muscular sac destined to lie close under the skin should actually arise from epiderm. But the want of uniformity is the puzzle, and meantime, apart from *Crossaster* and *Solaster*, the position is that in *Asterina* (13), *Cribrella* (19), *Echinus* (15), *Ophiothrix* (14) and *Echinocardium* (17) a cœlomic origin is assigned to the sac, while in *Porania* (9), *Asterias rubens* (8) and *A. vulgaris* (4a) the sac is said to be of mesenchymatous origin, and to be developed from a cell or cells appearing close under the epiblast. In Enteropneusts, Bateson (1a) and

Morgan (20) speak for a mesenchymatous, and Spengel (25) and Bourne (2) for an epidermal origin of the pericardial sac with which the madreporic vesicle of Echinoderms is no doubt homologous. To suggest that in the Solasters the madreporic vesicle corresponds to an enteropneust neural cavity which has somehow replaced a closely adjacent pericardium of enterocœlic or mesenchymatous origin is a speculation hardly stranger than the actual ontogenetic facts.

As a matter of fact, in *Crossaster papposus* and *Solaster endeca* the pit of origin of the madreporic vesicle is continued ventrally along a distinct ectodermal groove, from the bottom of which ectodermal cells are budded off towards the wall of the future epigastric cœlom. I have not yet been able to ascertain the fate of these cells, but certainly they do not originate in the epigastric cœlomic wall. Perhaps they are the fundament of the aboral nervous system, and correspond with the posterior dorsal nodes described by me in the larva of *Porania* (9, p. 42).

(c) Origin of Pharyngeal or Perioral Cœlom.—*Crossaster* agrees with *Cribrella* and *Solaster* in having this cœlom arising as a series of pockets from the posterior cœlom, one in each interradius. On the other hand, in *Asterias rubens* (8), *Asterina* (13) and *Asterias pallida* (11) the pharyngeal cœlom arises by a single outgrowth in the neighbourhood of interradius I/II. The fact that in *Crossaster* the pharyngeal outgrowth in interradius I/II does not lose its connection with the posterior cœlom goes some little distance on the way to reconcile the above divergences. We may see in these facts an indication borne out by other data that interradius I/II is to be counted as the first or fundamental interradius in Asteroid symmetry. In *Crossaster* the interradial origin of the pharyngeal cœlom is rendered in some respects more difficult, but in other respects easier to demonstrate by the fact that the development of the series of pockets is spread over a relatively long period.

(d) Origin of External Oral Perihæmal Ring.—*Crossaster* agrees with *Solaster* (7), *Asterias rubens* (8)

and *Cribrella* (10) in having all the pockets for this sinus arising from the posterior cœlom. On the other hand, in *Asterina* (13), *Ophiothrix* (14) and *Cribrella* (19) perihæmal pocket I/II is described as arising from the axial sinus portion of the anterior cœlom. In all probability the apparent discrepancy is related to the fact that a communication is established between the anterior cœlom and the dorsal horn of the posterior shortly before the formation of the perihæmal pocket in question. Indeed, in *Cribrella* (10) I have demonstrated the posterior cœlomic origin of this pocket. It seems in every way probable that primitively the whole of the perihæmal pockets arise from the left posterior cœlom. In *Echinus* all five pockets for the lantern cavity—a cavity which MacBride holds to be homologous with the external oral perihæmal sinus—take origin from the left posterior cœlom (15), while the corresponding pockets in *Echinocardium* have a similar origin (17).

(e) The Sequence in the Formation of the Hydrocœle Pouches.—In this connection the most striking feature is that while pouches I to V arise practically at the same time and VI very slightly afterwards sinistral to V, the remaining pouches arise partly in series sinistral¹ to V and partly in series dextral¹ to I. In *Solaster endeca* the pouches additional to the five primary ones either all arise in series sinistral to V (eight-rayed specimens), or the last of them arises (nine-rayed specimens) dextral to I from the dorsal horn of the hydrocœle crescent (10). We can say that there is a tendency towards secondary bilateral symmetry in the development of the later hydrocœle pouches of *Crossaster* (see Pl. 10, figs. 7 and 8). At the same time the two great landmarks of starfish radial asymmetry, namely, the madreporic complex and the anus in interradii I/II and V/VI respectively, show that, in *Crossaster*, rays VI to XII, like VI to IX in *Solaster*, are to be regarded as a secondary addition, and that the other rays are rightly numbered by

¹ See note on p. 156.

counting the madreporic interradius as I/II, with I on the dextral side of the madreporic opening.

Relation of Stalk and Sucker to Hydrocœle Ring.—It is significant to note (p. 161) that in *Crossaster* and *Solaster* the last remains of the sucker are external to the hydrocœle ring, which never actually encircles the larval stalk, as it does in *Asterina* (13) and *Asterias* (8). The difference is probably due to the late period at which the hydrocœle ring is completed in *Crossaster*, though this reason cannot apply in the case of *Cribrella*, where the ring in question is closed at an early stage without enclosing stalk or sucker. There is, however, every ground for thinking that Echinoderm larvæ with a large open hydrocœle crescent (*Asterina*, *Asterias*, *Crossaster*, *Solaster*) are more primitive in this respect than those in which the hydrocœle ring is closed practically from the first.

SUMMARY AND CHRONOLOGY OF DEVELOPMENT.

Segmentation total, equal or subequal (1 to 2 days). Formation of hollow blastula by egression (3 to 4 days). Formation of gastrula by invagination (5 to 6 days). Elongation of gastrula and division of archenteron into anterior, middle and posterior larval cavities (7 to 8 days). (In course of later development the anterior larval cavity gives rise to cavity of præoral lobe, hydroporic canal, hydrocœle, epigastric cœlom, axial sinus, stone-canal, axial organ, internal oral perihæmal ring, and oral hæmal ring. The middle larval cavity gives rise to all portions of the adult digestive cavity. There is no larval mouth, œsophagus or anus. The posterior larval cavity gives rise to the hypogastric cœlom, the pharyngeal or perioral cœlom, the external oral perihæmal ring, the "genital rachis" and the aboral perihæmal sinus.) Indication of brachia and sucker (9 to 10 days). Formation of hydroporic opening (11 to 12 days). Closure of blastopore; formation of dorsal sac or madreporic vesicle from epiblast (12 to 14 days). Hydrocœle pouches I-VI

appear (15 to 17 days). First indication of developing aboral and ambulacral skeletal plates (17 to 18 days). Flexion and torsion of præoral lobe begins (18 to 19 days). Ultimately the preoral lobe is absorbed or incorporated with the oral (larval left) side. Sucker fixation (19 to 20 days). The hydrocœle lobes appear externally in the following sequence: II-IV (21 to 22 days), I (22 to 23 days), VII (27 to 28 days), XII (29 to 30 days), VIII (33 to 34 days), IX and XI (37 to 41 days), X (43 days). First pairs of sucker feet on rays I-VI begin to be functional and the larvæ shift position slightly while still anchored by the sucker (28 to 30 days). Sucker fixation lost (35 days). Mouth opening (38 to 42 days) and anal opening (49 to 55 days) appear. The oral and aboral gastric ligaments arise by partial breaking down of the mesenteric sheets separating the perioral and hypogastric cœloms from the hypogastric and epigastric cœloms respectively.

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EXPLANATION OF PLATE 10,

Illustrating Dr. James F. Gemmill’s paper on “The Development of the Starfish *Crossaster papposus*, Müller and Troschel.”

My paper on the development of *Solaster endeca* (7) may be referred to for figures which illustrate the following features in the development of *Crossaster papposus*: Segmentation, blastula and gastrula formation, Pl. i, figs. 1-6; separation of primary cavities in the larva, Pl. iii, figs. 24-33; general growth and mode of attachment of the larva, Pl. ii, figs. 15-21; sections of larvæ and of stages in metamorphosis, Pl. iv, figs. 36-48; various points in the development of the skeleton, Pl. i, figs. 8 and 9, and Pl. ii, fig. 30.

ABBREVIATIONS EMPLOYED IN REFERENCE LETTERS BOTH IN
PLATE AND IN TEXT-FIGURES.

a.a. Anterior brachium. *a.c.* Anterior larval cœlomic cavity. *amp.* “Ampulla of stone-canal” (see p. 172). *ar.* Aboral arm-rudiment. *ax.o.* Axial organ. *ax.s.* Axial sinus. *ax.p.* Main opening from axial sinus into pore-canal system. *bl.* Blastopore. *br.* One or other of the lateral brachia. *cbr.* Cavity of præoral cœlom running up into a brachium. *cl.d.* Left lateral diverticulum of anterior larval cœlomic cavity. *d.h.* Dorsal horn of posterior cœlomic cavity. *d.s.* Dorsal sac or madreporic vesicle. *ect.* Ectoderm. *ep.c.* Epigastric cœlom (right lateral diverticulum of anterior larval cœlomic cavity). *g.* Enteron. *g.h.t.* Gastric hæmal tufts. *hy.* Hydrocœle. *hyd.* Hydroporic canal or opening. *hyp.c.* Part of hypogastric cœlomic cavity. *m.a.p.* Cushion over mouth-angle plates carrying spines. *mlh.* Mouth. *mes.*